Microevolutionary Response in Lower Mississippian Camerate Crinoids to Predation Pressure

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By

Jeffrey R. Thompson
The Ohio State University
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Project Advisor: Dr. William I. Ausich, School of Earth Sciences

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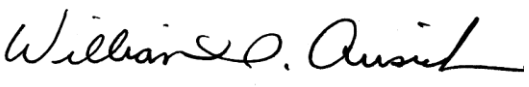

William I. Ausich, Advisor
School of Earth Sciences

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Abstract

Crinoids were relatively unaffected by the end-Devonian Hangenberg event, but the major clades of Devonian durophagous fishes suffered significant extinctions. These dominant Devonian fishes were biting or nipping predators. In response to the Hangenberg event, Lower Mississippian crinoids underwent an adaptive radiation, while fish clades with a shell-crushing durophagous strategy emerged. Durophagous predators are inferred to have been more effective predators on camerate crinoids and it is hypothesized that through the Lower Mississippian, camerate crinoids evolved more effective anti-predatory strategies in order to compensate for the more effective predatory strategy of the durophagous fishes. More convex plates and longer spines are commonly regarded to provide more effective anti-predatory strategies. Did convexity and spinosity increase among camerate crinoids during the Lower Mississippian? A new method was formulated to test for an increase in convexity of the calyx plates among species of the genus *Agaricocrinus*. Spine length was analyzed in the genera *Aorocrinus* and *Dorycrinus* and is a simple linear measurement standardized to calyx diameter. Data were analyzed using Kolmogorov-Smirnov and Mann-Whitney *U* tests to determine if morphological change was statistically significant. *Dorycrinus* showed the most significant evidence for directional change through time, which provides evidence for escalation as a response to fish predation. *Aorocrinus* seemed to most likely display stasis or a random walk, whereas *Agaricocrinus* did not show evidence for distinct directional evolution, but rather showed a decrease in variance in convexity values through time.

Introduction

The hypothesis of escalation as originally proposed by Vermeij (1987) and later tested by Kelly and Hansen (1993) posits that through time, as biological hazards, in the form of increased fitness of a predator, become more severe, adaptations to these hazards in other taxa become more greatly expressed. During the Early Mississippian Period, following the End-Devonian Hangenberg extinction event, durophagous fish generic diversity and camerate crinoid generic diversity increase in concert, until camerate diversity declined during the Viséan (Sallan et al. 2011). Many Mississippian camerates displayed increased plate convexity and spinosity compared to their Devonian counterparts. These legacy adaptations (Sallan et al. 2011) represent traits that were once selectively beneficial during the Devonian, but subsequently became obsolete and did not transition to new optimum conditions(Sallan et al. 2011). Spinosity and plate thickess first appeared during the Mid-Paleozoic Marine Revolution (MPMR) (Meyer and

Ausich, 1983, Signor and Brett, 1984, Brett and Walker, 2002), and are inferred to have evolved as an anti-predatory strategy. Huntley and Kowalewski (2007) documented that mean predation frequencies determined from predation traces and global mean generic level diversity track each other through the Phanerozoic. This supports the hypothesis that through the Lower Mississippian, camerate crinoid anti-predatory adaptations such as plate convexity and spine length may increase through time in concert with generic level diversity. Escalation following the Hangenberg event could be expected given that Vermeij (1987) suggested that escalation may be common during times of changing environmental conditions. This line of thinking was also supported by the work of Kelly and Hansen (1993) who concluded that drilling frequencies in gastropods and bivalves increased following extinction events at the Cretaceous-Paleocene and Eocene-Oligocene boundaries. In this project, spinosity and plate convexity in three genera of camerate crinoids will be tracked through the Lower Mississippian to examine whether escalation occurs in crinoids due to durophagous predation.

Background

Sallan and Coates (2010) concluded that the Hangenberg extinction event at the Devonian-Carboniferous boundary represented a faunal turnover for gnathostomes. Whereas the Devonian was dominated by placoderms, sarcopterygians, and acanthodians, the Mississippian was marked by rises in generic level diversity in chondrichthyes, actinopterygians, and tetrapods (Sallan and Coates, 2010). Sallan and Coates (2010) also examined species-level faunal composition for 66 geographically widespread gnathostome localities and determined that Devonian and Mississippian localities are compositionally distinct with regard to gnathostome faunas. This vertebrate turnover had an increase in durophagous vertebrates with a crushing dental morphology, compared to dominant shearing dental morphology of the Devonian (Sallan

and Coates, 2010). At the end of the Tournasian, 51% of chondrichthyans were crushers, whereas in the Famennian, only 21% of chondrichthyans displayed a crushing dental morphology (Sallan and Coates, 2010).

Crinoids underwent a major extinction at the Givetian-Frasnian boundary that decreased crinoid generic diversity by approximately one third (Baumiller and Messing, 2007). Following this extinction event, crinoid diversity underwent an almost constant gain as crinoids passed through the Frasnian-Famennian Kellwasser event relatively unscathed (Waters and Webster, 2009). While vertebrates were undergoing a significant faunal turnover, crinoids were relatively unaffected by the Hangenberg event and diversity underwent a sharp rise from the Famennian to the Tournasian (Kammer and Ausich, 2006, Sallan et al. 2011). Camerate crinoids exhibited increased diversity until the Viséan when camerate diversity began to decline continuing through the rest of the Mississippian. Thereafter, crinoid faunas became dominated by advanced cladids (Kammer and Ausich, 2006). Kammer and Ausich (2006) attributed the increased diversity of camerates during the Tournasian and into the Viséan to newly abundant carbonate ramp environments, ideal for carbonate environment-preferential camerates (Kammer, 1985, Kammer and Ausich, 1987), following the demise of Frasnian-Famennian rimmed shelf environments (Kammer and Ausich, 2006). They additionally proposed that the demise of camerates beginning during the Viséan was due to their inability to cope with the increase of siliclastic input into the oceans in the Middle to Late Mississippian (Kammer and Ausich, 2006). Sallan et al. (2011) proposed that the decline in camerate crinoid generic diversity was due to camerates' inability to defend themselves adequately in the face of the new Mississippian durophagous vertebrates. Both factors undoubtedly played a role (Ausich and Kammer, 2013); and in this study, the expression of defensive phenotypic traits in three genera of camerate crinoids are examined to

test for escalation in the interval leading up to the decline of camerate generic diversity in the Viséan.

Crinoid-Fish Ecological Interactions during the Early Mississippian

In order to test for escalation in the fossil record, it is necessary to demonstrate a predator-prey relationship between the proposed predator and prey. Much evidence exists in the fossil record to indicate that crinoids fell prey to durophagous fish. Waters and Maples (1991) attributed the predatory pressures on crinoids during the Carboniferous to holocephalans. Holocephalans were primarily bottom feeding and durophagous, and they reached their peak diversity during the Carboniferous (Moy-Thomas and Miles, 1971a). Malzahn, (1968) noted that the Permian petalodontid holocephalan *Janassa bituminosa* was stenophagous, or fed on a limited variety of food. Its stomach contents included brachiopod shell fragments, foraminifera, fragments of crabs, and most importantly for this study, crinoid arm plates. Zangerl and Richardson (1963) reported crinoid columnals from a Pennsylvanian coprolite, although they posited that columnals must be a poor source of food and were unable to tell if the crinoid was prey or if the columnals were ingested from the substrate. In addition to this direct evidence of fish and crinoid predator-prey relationships in the fossil record, Laudon (1957) noted the co-occurrence of Mississippian encrinites with bone beds filled with durophagous shark teeth. Teeth of durophagous fish from the Mississippian of North America have also been known to occur in the same formations as crinoids since the work of St. John and Worthen (1875).

Evidence of regeneration is also a telltale sign of non-lethal predation against crinoids. Lane and Webster (1966) noted irregularities in the arms of cladid crinoids indicative of regeneration due either to breakage from rough water conditions or predation and Lane (1984) figured a regenerated anal sac of the cladid crinoid *Cyathocrinites sp.* from the Ramp Creek

Formation of Montgomery County, Indiana. Springer (1920) also noted a case in which a specimen of the species *Taxocrinus colletti* White 1881 was able to regenerate its entire crown above the basal plates, presumably as a response to an episode of predation. Of relevance to this project, Hattin (1958) figured a regenerated spine from the Pennsylvanian crinoid *Lobalocrinus wolforum* Moore & Plummer 1940. Furthermore, Baumiller and Gahn (2004, 2013) and Gahn and Baumiller (2005, 2010) gave an extensive treatment to the issue of regeneration in crinoids, finding evidence of regeneration in crinoids from the Ordovician to the Pennsylvaian (Baumiller and Gahn, 2004), with a special emphasis on the Lagerstätte from the Tournasian of LeGrand Iowa (Gahn and Baumiller, 2005).

The Mississippian is known as the "Age of Crinoids" because it is during the Mississippian that crinoids reach their peak phanerozoic diversity (Kammer and Ausich, 2006). The Mississippian is also characterized by the presence of widespread pelmatozoan dominated communities that appeared during the Tournasian (Kammer and Ausich, 2006). These pelmatozoan "crinoid gardens" are realized in the rock record in the form of widespread regional encrinites (Ausich, 1997) that were especially common during the Early Mississippian. Given the widespread nature of these encrinites and thus the abundance of crinoids on the seafloor, it is reasonable to conclude that crinoids may have been a major food source for Mississippian durophagous predators. Because most of the arms and stem of crinoids are calorically deficient $CaCO_3$, it is unclear how energetically effective crinoids would have been as prey. Despite the low energetic benefits of much of the crinoid skeleton, several lines of evidence have been proposed to explain predation on crinoids. Lane (1984) hypothesized that camerate crinoids likely housed their gonads within their plated thecae. Thus, a gravid crinoid would be more calorically satisfying to a predatory fish and therefore would be more likely to be prey (Lane,

1984). Fish predation on crinoids may also not be direct predation but rather collateral damage as a result of fish predation on crinoid infestors (Meyer, 1985, Baumiller and Gahn, 2002, Gahn and Baumiller, 2005), such as platyceratid gastropods (Brett and Walker, 2002, Brett 2003). It was first proposed that platyceratid gastropods attached to crinoid anal tubes were engaging in the act of coprophagy (e.g., Hinde 1885, Bowsher, 1955, Lane, 1984, Meyer and Ausich, 1983) Lane (1984) proposed that these platyceratids were gametophagous and were attempting to eat gametes released from the anal vent. More recently it has been proposed (and tested by Baumiller, 2002 and Gahn and Baumiller, 2003) that platyceratids were gastrophagous. They stole food from the ambulacral food grooves of their crinoid hosts and they attached to and occasionally drilled into the calices of the crinoids (Baumiller, 1990, 2002, Baumiller and Gahn, 2002, Gahn et al. 2003, Gahn and Baumiller, 2003). These traces and especially the reaction rims surrounding them further serve as evidence that infestors were living on crinoid thecae (Gahn et al. 2003). Brett (2003) provided evidence that platyceratid gastropod infestation is associated with crinoids displaying spinosity during the Devonian. This may support the hypothesis that crinoid predation is due to collateral damage, or it may indicate that spinosity arose in certain lineages in order to deter platyceratid infestation.

In addition to observed evidence of predation in the fossil record, inferred evidence also exists with the appearance of spines and increased thickness of plates in response to the appearance of durophagous predators in the MPMR (Meyer and Ausich, 1983, Signor and Brett, 1984, Brett and Walker, 2002). Signor and Brett (1984) proposed that with the evolution of durophagous predators during the Devonian, crinoids evolved thicker calyx plates and more spinose calices in order to repel predation from durophages. Baumiller and Gahn (2013) treated regeneration in crinoids as evidence of sublethal predation and thus used it to infer predation

pressures on crinoids in both the Paleozoic and the modern. Their data indicated that Lower Mississippian crinoids experienced lesser predation pressure than modern crinoids, supporting Vermeij's (1987) hypothesis that predation pressures increased through time. Baumiller and Gahn (2004, in supplemental online material) additionally concluded that in examining regeneration frequencies from crinoid Lagerstätten through time, arm regeneration frequencies in camerate crinoids increased from 12.4 during the Tournasian of LeGrand, Iowa (time bin 1 in Kammer and Ausich (2007)) to 18.2 during the Viséan of Crawfordsville, Indiana (time bin 6 in Kammer and Ausich (2007)). Baumiller and Gahn (2004) concluded that this increase in regeneration frequency was not statistically significant; however, in the light of evidence for increased predation pressure provided by Sallan et al (2011), the role of predation during this time interval should be examined more closely. Vermeij (1982) noted that because unsuccessful or non-lethal predation is responsible for selection on anti-predatory traits, it is only the individuals who survived predatory encounters who will go on to reproduce. Under this line of thinking, heightened regeneration frequencies in crinoids from the Tournasian to Viséan (Baumiller and Gahn, 2004, in online supplemental material) may be good evidence of increased predation pressure.

Sallan et al. (2011) demonstrated that following Hangenberg event, camerate crinoid generic diversity mirrored that of Mississippian durophagous fishes, until the Viséan when camerate diversity and durophagous fish diversity were strongly negatively correlated. Sallan et al. (2011) attributed this initial mirroring of diversity to independent radiations, however, given that Huntley and Kowalewski (2007) found a correlation between predation pressure and diversity through the Phanerozoic, it is possible that the simultaneous rise in durophagous fish and camerate crinoid diversity may be due to escalation. If this is the case, the proposed rise in

diversity would be expected to mirror escalation on the microevolutionary level, in the form of more convex plates and longer spines as new species of camerates arose through the Lower Mississippian. Sallan et al. (2011) attributed the eventual decline in camerate diversity to camerates inability to effectively repel more derived Mississippian durophagous fish with Devonian legacy adaptations. Herein, I test the hypothesis that microevolutionary escalation (more convex plates and longer spines) in Early Mississippian camerate crinoids explains the mirroring of diversity in durophagous fish and camerate crinoids following the Devonian-Mississippian Hangenberg event.

Methods

Three genera, *Agaricocrinus*, *Dorycrinus,* and *Aorocrinus,* were chosen for analysis based on their long stratigraphic ranges through the Lower Mississippian and their easily quantifiable anti-predatory traits. *Agaricocrinus* has nodose tegmenal calyx plates that can be used to track changes in plate convexity, and *Agaricocrinus* and *Dorycrinus* both have tegmenal spines. The three examined genera belong to the monobathrid camerate family Coelocrinidae. Specimens were photographed and measured from the National Museum of Natural History (NMNH), The Ohio State University Orton Geological Museum (OSU), The Cincinnati Museum of Natural History (CMCIP), The Field Museum of Natural History (FMNH), and the University of Illinois (RX). A few measurements were also taken from the systematic literature including Laudon et al. (1952) and Ausich and Kammer (1991). These measurements were obtained through photo measurement. Spine length is a simple linear measurement and thus, spine length measurements from specimens of *Dorycrinus* and *Aorocrinus* were obtained through direct measurement with calipers. One spine on the top of the tegmen in *Aorocrinus* was examined in addition to three spines on the tegmen of *Dorycrinus*. One of these spines is located in the center

of the tegmen, and two are on the tegmen above the arm rays in the C and E ray. All spine lengths are reported as standardized to the calyx diameter of the specimen from which they were measured.

Plate convexity measurements for *Agaricocrinus* specimens were obtained by photographing specimens and refining the data through morphometric analysis. Photographs of each plate were taken along a consistent axis in order to maintain concordance through all photos. For each specimen of *Agaricocrinus*, (except those from The Ohio State University) two plates were photographed. These plates are herein designated as peristomial cover plate 1 (PS1) and peristomial cover plate 3 (PS3) from Kammer et al. (2012) modified from Sumrall and Waters (2012). All PS1 photographs were taken with the camera lens angled down an axis passing through the A ray to the C-D interray. All PS3 photographs were taken down an axis passing through the A-E interray to the C ray. Both peristomial cover plates in each individual were photographed twice. After the first photograph was taken, the orientation of the calyx was moved and then readjusted to the original orientation before taking the second photograph.

Because it is necessary to convert photographic data into numerical data in order to perform statistical analyses, the convexity value of each photographed plate was determined by modeling the outline of the cross sectional view of the plate and fitting a parabola to this modeled outline using the computational software package MATLAB® (The Mathworks inc., 2012). The cross sectional view of the plate was modeled by using an algorithm that traces the outline of the plate by plotting points where the RGB pixel values of the photograph change from those of the color of the crinoid calyx to those of the photograph's background. A 2^{nd} order polynomial was then fitted to this modeled plate outline (Figure 1). When the parabola is fitted to the modeled plate outline, MATLAB gives an output consisting of the equation for the parabola,

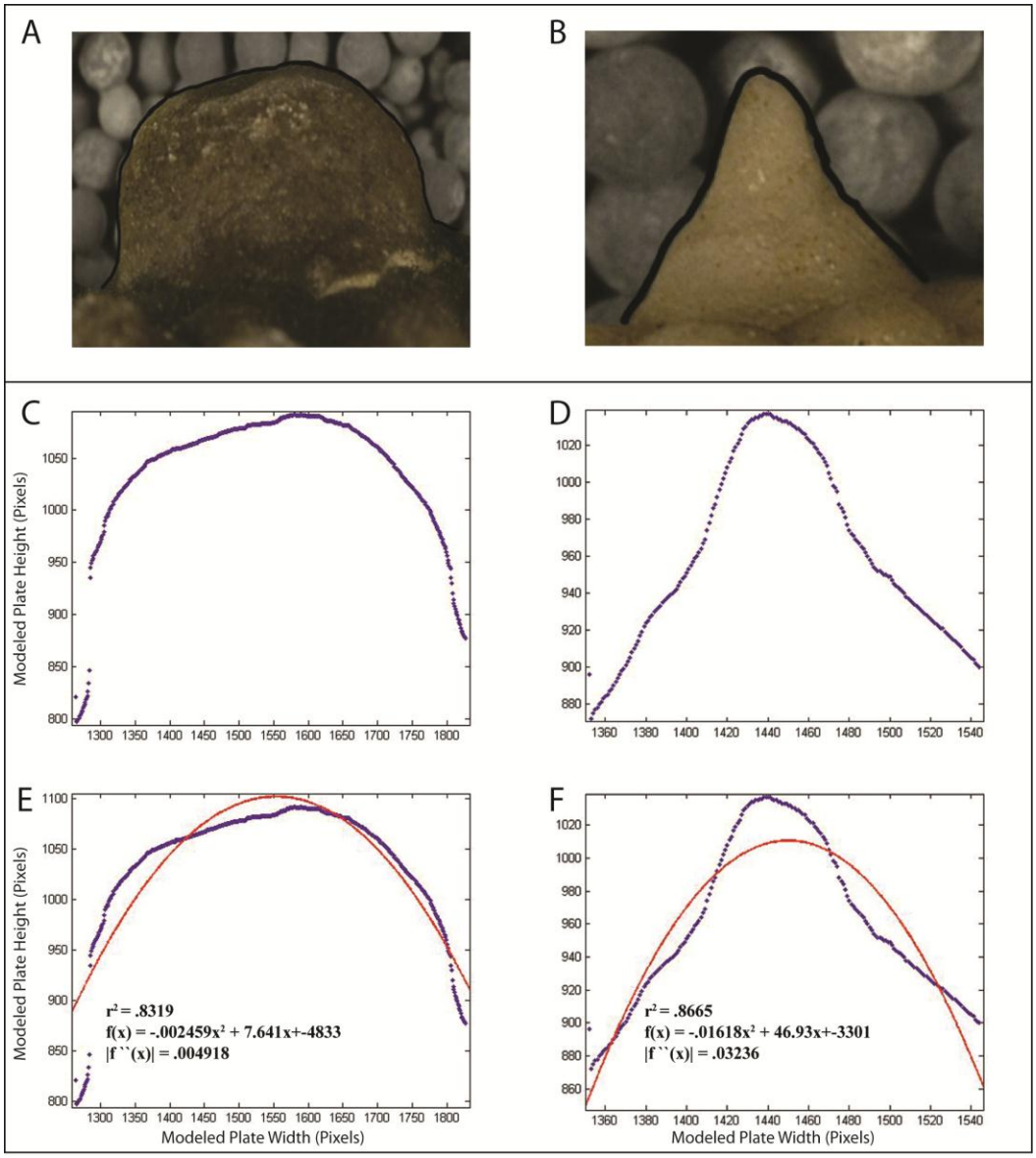

Figure 1. Parts A-F demonstrate method to determine convexity in two different specimens.

an r^2 value representing how well the parabola fits the modeled data, and an adjusted r^2 value(The Mathworks inc, 2012). The second derivative of the equation representing the parabola was taken in order to determine the concavity of each parabola. The second derivative of a parabola is equal to the concavity of the parabola; however, because the fitted parabolas are concave down, the second derivative is negative and may be referred to as the convexity. Thus, in order to make these values positive, and available for statistical analysis, it is necessary to take the absolute value of the convexity values. The resulting units of the second derivative are

reported in pixels^{-1}. Although not all photographs were taken at a consistent distance from the specimen, when comparing photographs taken at different magnifications, the best fit parabolas scale isometrically allowing for sound analysis of data taken at different magnifications. Convexity is deviation from flatness of a shape, and this is used here to examine how plates change from flat, non-nodose plates, to more nodose, and spine-like convex plates. Because two convexity values were determined for each plate, the average of each of these two values was taken to account for slight differences in convexity values due to slight variation in photographic axis orientation and morphometric algorithm output.

For statistical analysis, specimens were organized into time units as defined by Ausich and Kammer (2006) and refined by Kammer and Ausich (2007). Of Ausich & Kammer's eleven time units of Mississippian crinoid occurrences spanning from the base of the Tournaisian to the top of the Serpukhovian this study only examined specimens from the time bins 1, 3, 4 and 6, spanning from the Tournaisian to the Viséan. Analyses were performed on convexity values for PS1 and PS3 in *Agaricocrinus*, in addition to spine length/calyx diameter values in *Aorocrinus* and central, C-ray, and E-ray spines in *Dorycrinus*. Mann-Whitney *U* tests were run on distributions between traits in each time bin. For the Mann-Whitney *U* tests, H_0 was that the distributions were the same and H_a was that the distribution from the younger time bin was greater than the distribution from the older time bin. Bootstrapped two-way Kolmogorov-Smirnov tests (Sekhon, 2011) (number of bootstraps=1000) were also performed on disribution functions of consecutive trait value distributions between each time bin, where H_0 was that the distributions from each consecutive time bin were drawn from the same distribution, i.e. the distributions were the same and H_a was that the younger distribution was drawn from a greater population than the older population, i.e. has a greater distribution function. Mean convexity

values of all species of *Agaricocrinus* during each time bin are reported in Table 1. Mean spine length/calyx diameter values of all species of *Aorocrinus* are reported in Table 2. Mean spine length/calyx diameter values for *Dorycrinus* are reported in Table 3. Mean values for each time bin are reported in Table 4. Results of Mann-Whitney *U* tests are reported in Table 5. Results of Bootstrapped Kolmogorov-Smirnov tests are reported in Table 6. All statistical analyses were run in R (R Core Team, 2012).

Results

Convexity in Agaricocrinus.—Comparison of trait means of PS1 between time bin 1 and time bin 3 indicate that the increase in trait values between time bin 1 and time bin 3 is statistically significant (Mann-Whitney U Test: U=170 p-value=0.0113). Additionally the bootstrapped comparison of distributions indicates that the distribution in time bin 3 is the same as the distribution in time bin 1 (Bootstrapped Kolmogorov-Smirnov test: D=0, Bootstrapped p-value=1.0). Between time bin 3 and time bin 4 there is no statistically significant increase in trait values (U=640 p-value=0.9955). Additionally, the bootstrapped comparision between distributions in time bins 3 and 4 indicate that the distributions increased between time bin 3 and time bin 4 (D=0.3619, bootstrapped p-value=0.002). Distributions in time bin 4 and time bin 6 also have an increase in the distributions (D=0.4151, bootstrapped p-value=0), but there is no statistical support for an increase in trait values between time bins 4 and 6 (U=1175 p-value=1.0).

For distributions and means for trait values of PS3, there is statistical support for an increase in trait values between time bin 1 and 3 (U=210 p-value=0.007066), and the distributions were shown to be the same between the two time bins (D=0, bootstrapped p-value=1). Distributions in time bin 3 and time bin 4 are the same (D=0.0694, bootstrapped p-

value=0.734), and there is little statistical support for an increase in the trait values between the two time bins (U=882 p-value=0.3369). Analyses indicate that there is little statistical support for an increase in trait values between time bins 4 and 6 (U=1322, p-value=0.9719) and comparison between the distributions indicates that the distributions are the same (D=.1986, bootstrapped p-value=0.83). The sample sizes in time bin 1 relative to other time bins for both PS1 (n=5) and PS3 (n=7) are small, thus the observed increases in trait means in both PS1 and PS3 between time bins 1 and 3 may be caused by these low sample sizes. Comparisons between distributions in time bins 1 and 3 may also be affected by this small sample size.

Spine Length/Calyx Diameter in Aorocrinus.—After analysis, it appears that there is no consistent trend in either the distribution shapes or distribution means in the spine length/calyx diameter values of *Aorocrinus*. When time bin 1 was compared to time bin 3, there was no statistically significant increase in trait mean values (U=20, p-value=0.8465), and the comparison of the distributions indicated that there may be an increase in the probability distribution functions between time bins 1 and 3 (D=0.6667 bootstrapped p-value= 0.029). If the trait values in time bin 3 and time bin 4 were compared, there was no statistical support to indicate that the values increased from time bin 3 to time bin 4 (U=16, p-value=1), and if the probability distribution functions of the distributions were compared, there is evidence that the distributions increased from time bin 3 to time bin 4 (D=.8619: bootstrapped p-value= 0). The comparisions between time bin 4 and time bin 6 indicate that their distributions are the same (D=0, p-value=1) or that the trait values of the distribution increased from time bin 4 to 6 (U=50, p-value=0.09297).

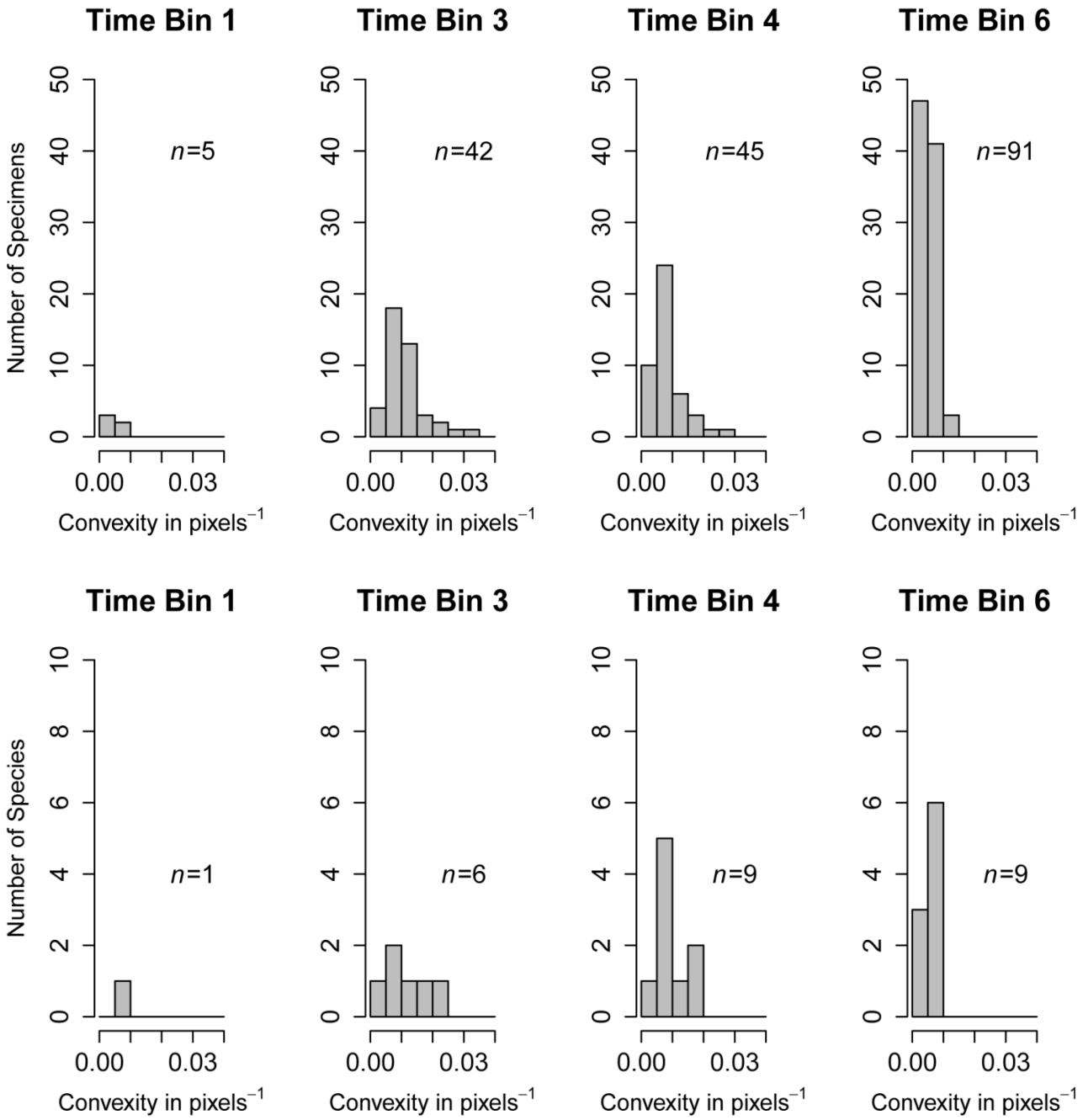

Figure 2. Histograms of mean convexities of PS1 of species of *Agaricocrinus* in time bins 1 through 4.

Spine Length/Calyx Diameter in Dorycrinus.—Spine length/calyx diameter values in the central spine in *Dorycrinus* indicate that there is no significant change in the distribution functions between time bins 3 and 4 (D=0.3, bootstrapped p-value= 0.182) and 4 and 6 (D=0.1667, p-value= 0.607). Additionally, there is no statistically significant change in the values of the

distributions between time bins 3 and 4 (U=213, p-value=0.119) and 4 and 6 (U=89, p-value=0.2306). The analyses of spine length/calyx diameter values from the C ray show no change in the distributions (D=0 boostrapped p-value=1) and increase in trait values of the two distributions (U=60 p-value=0.0001249) between time bins 3 and 4 and a lesser change in trait values (U=67, p-value=0.04742) and a non-significant change in the distribution functions (D=0.0667, bootstrapped p-value=0.884) between time bins 4 and 6. The analyses of the spine length/calyx diameter values of the E ray indicate there was no statistically significant increase in trait values between time bins 3 and 4 (U=19, p-value=.366) and a non-significant change in the corresponding distribution functions (D=.25, bootstrap p-value=.7). The distribution functions for E ray values between time bins 4 and 6 are equal (D=.0796, bootstrapped p-value=.83), yet the values in time bin 4 are statistically significantly equal to the values in time bin 6 (U=.001755, p-value=0.956).

Species	Convexity of PS1 in pixels $^{-1}$	*n*	Convexity of PS3 in pixels^{-1}	*n*	Time Bin	Average Age of Time Bin (in MYA)
Agaricocrinus americanus	0.005757068	44	0.007309988	34	6	344.6
Agaricocrinus acugelarus	0.020165	1	0.02997	1	3	344.6
Agaricocrinus bellatrema	0.006208	5	0.008187143	7	4	346.05
Agaricocrinus brevis	0.011582105	19	0.006817458	12	3	350.6
Agaricocrinus bullatus	0.00679525	8	0.01036125	8	4	346.05
Agaricocrinus conicus	0.004259	4	0.005581	3	6	344.6
Agaricocrinus convexus	0.016361	2	0.0090305	2	4	346.05
Agaricocrinus crassus	0.0036181	10	0.005376167	6	6	344.6
Agaricocrinus illinoisensis	0.005202	1	0.0097755		3 or 4	350.6 or 346.05
Agaricocrinus excavatus	0.007138714	7	0.007105429	7	4	346.05
Agaricocrinus fiscellus	0.01645775	8	0.006155788	8	3	350.6
Agaricocrinus gracilis	0.0166468	5	0.012088	4	4	346.05
Agaricocrinus hodgsoni	0.013379333	3	0.005405733	3	3 or 4	350.6 or 346.05
Agaricocrinus illinoisensis	0.0046255	2	0.0056865	2	4	346.05
Agaricocrinus inflatus	0.005348833	6	0.00398715	4	4	346.05
Agaricocrinus iowensis	0.0050338	5	0.007421833	6	6	344.6
Agaricocrinus nodosus	0.0053819	5	0.0066758	5	4	346.05
Agaricocrinus nodulosus	0.00365475	8	0.004416663	8	6	344.6
Agaricocrinus nodulosus mcada	0.006058	1	0.007658	1	6	344.6
Agaricocrinus planoconvexus	0.0065578	5	0.003551028	5	3	350.6
Agaricocrinus praecursor	0.003221667	3	0.0099515	4	3	350.6
Agaricocrinus sampsoni	0.00523074	5	0.003743871	7	1	364.3
Agaricocrinus splendens	0.007688714	7	0.006734	6	6	344.6
Agaricocrinus stellatus	0.01328	5	0.008238	5	4	346.05
Agaricocrinus whitfieldi	0.00673	5	0.0074195	4	6	344.6
Agaricocrinus wortheni	0.005091571	7	0.00707075	8	6	344.6
Agaricocrinus pyramidatus	0.009296167	6	0.010232429	7	3	350.6
Agaricocrinus blairi	-	-	0.00902	1	3	364.3

Table 1. Mean convexity values for PS1 and PS3 in all examined species of Agaricocrinus.

Discussion

Following Vermeij's hypothesis of escalation (1987), it was expected that species of the examined camerate crinoid genera would undergo directional evolution in trait morphology and anti-predatory traits would become more greatly expressed through time as a response to

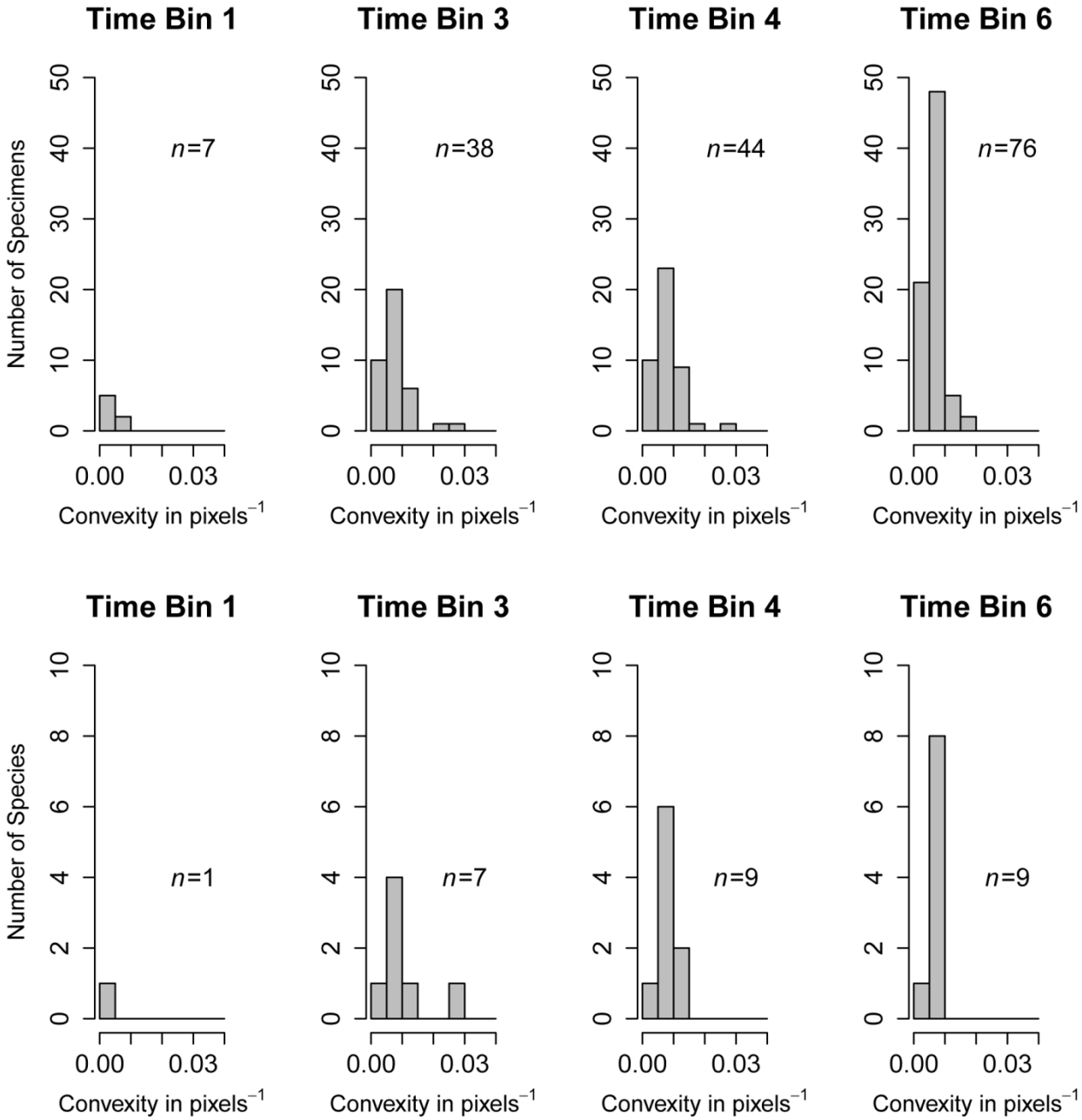

Figure 3. Histograms of convexity values of PS2 of specimens and mean convexities of species of *Agaricocrinus* in time bins 1 through 6.

durophagous fish predation. Of the observed taxa, only the genus *Dorycrinus* displays this trend. This occurs in two of the three examined traits. In *Agaricocrinus* both, traits observed, PS1 and PS3, have a statistically significant increase in plate convexity from time bin 1 to time bin 3 (although time may be spurious, see above). The sameness of the distributions as evidenced by these Kolmogorov-Smirnov tests may alsobe a function of the sample sizes consisting of less than 8 data points. Assuming this is not spurious, this could be indicative of evolutionary change due to predation pressure between time bins 1 and 3. Both distributions for PS1 and PS3 exhibit greater ranges of convexity values in time bins 3 and 4 than they do in time bin 6. This trend exists both when all specimens are examined together and when specimens are grouped into species (See Figures 2 and 3). Additionally, sample sizes in time 6 are larger, both in number of specimens and number of taxa, than in any other time bin. This may also indicate directional evolution toward either an anti-predatory optimum or a minimum threshold value, at which the anti-predatory efficiency of a convex plate is reached. If this is the case, it appears that these values would be centered around the mean convexity of each trait around 0.005 in PS1 and 0.007 in PS3. It is also important to note that Bootstrapped Kolmogorov-Smirnov tests of distributions of PS3 and Mann-Whitney *U* tests of PS3 trait values indicate that there is no statistical support for increased convexity values or changes in the distribution functions between time bins 3 and 4 and 4 and 6. This may be indicative of morphospace stasis in this trait in the genus *Agaricocrinus* from time bin 3 to time bin 6. Although because of a statistically significant increase in distribution functions of PS1 from time bin 3 to time bin 4, it may be likely that stasis was just occurring in PS2, and that the evolution of the organism as a whole may be a random walk.

In *Aorocrinus*, there is no statistically significant increase in spine length/calyx diameter values through time according to the Mann-Whitney *U* tests. According to the Bootstrapped

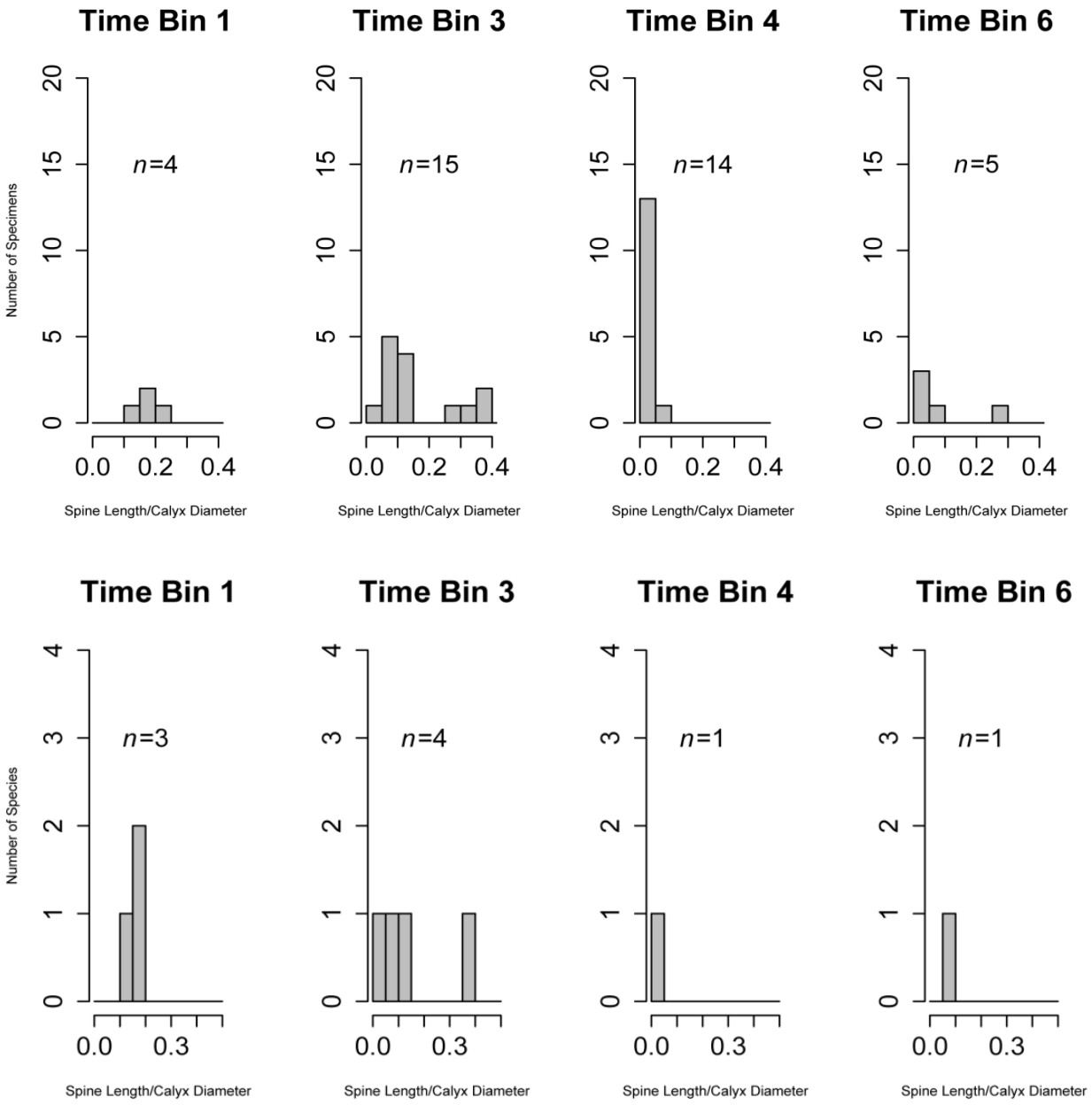

Figure 4. Histograms of spine length/calyx diameter of specimens and mean spine length/calyx diameter for species of *Aorocrinus* in time bins 1 through 6.

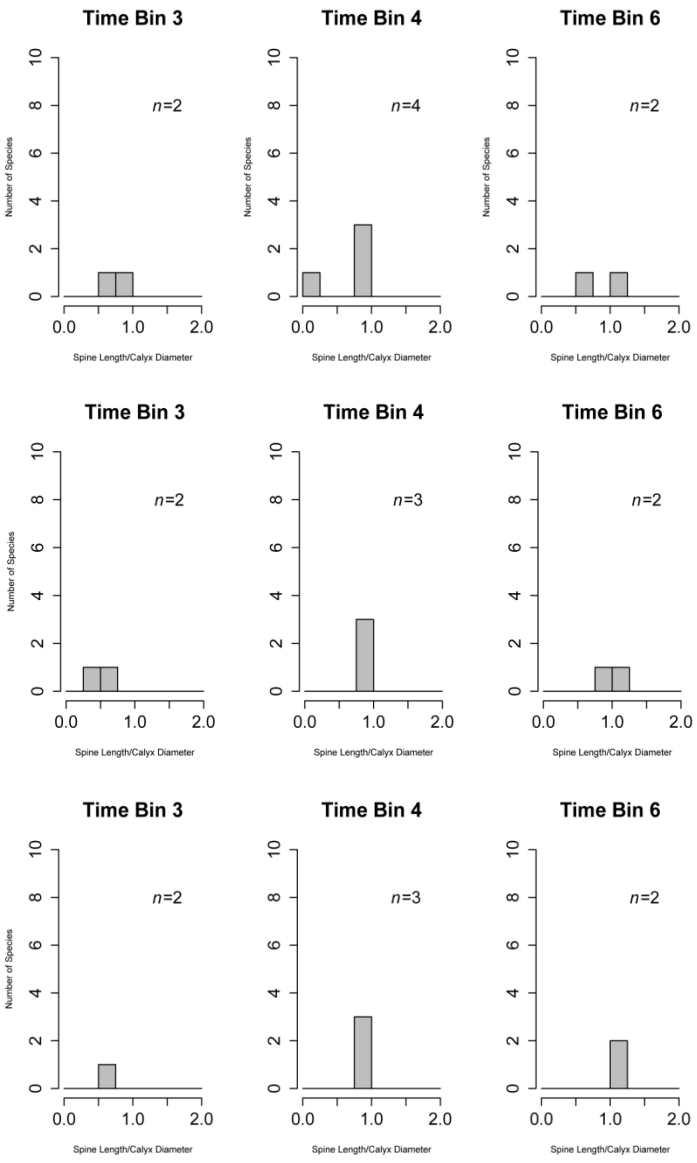

Figure 5. Mean spine length/calyx diameter for species of *Dorycrinus*

Kolmogorov-Smirnov test comparing time bin 1 and time bin 3, it appears that the probability distribution functions of the two distributions may be the same, which could be indicative of stasis between the two time bins. However, the sample size in time bin 1 is small (*n*=4), thus interpretation regarding comparisons between time bin 1 and 3 is tentative. Between time bins 3 and 4 there is a decrease in the range and a honing in on very low spine length/calyx values. This trend is because of the presence of *Aorocrinus* sp., which has a mean convexity value of 0.031 makes up all of the 17 examined individuals in time bin 4 (Figure 4). This is the most abundant species of *Aorocrinus* during time bin 4, thus the decrease in spine length/calyx values, coincident with the abundance of *Aorocrinus* sp. during time bin 4 may indicate that spine length in *Aorocrinus* was not a strong enough selective factor in driving evolution. Kolmogorov-Smirnov testing indicates that the distributions in time bins 4 and 6 were likely drawn from the same distribution, which could be indicative of stasis between the two time bins, although there is no statistically significant increase in trait values.

The ratio of spine length to calyx diameter of the central spine of *Dorycrinus* has no statistically significant increase in values through time (See Tables 3 and 4 in appendix). This may indicate a period of morphological stasis in this trait from time bins 3 to 6. If stasis is, in fact, occurring, then it is possible that predation pressure on these crinoids may not be strong enough to cause directional change in this trait, or that this trait may not provide increased fitness to individuals under increasing predation pressure.

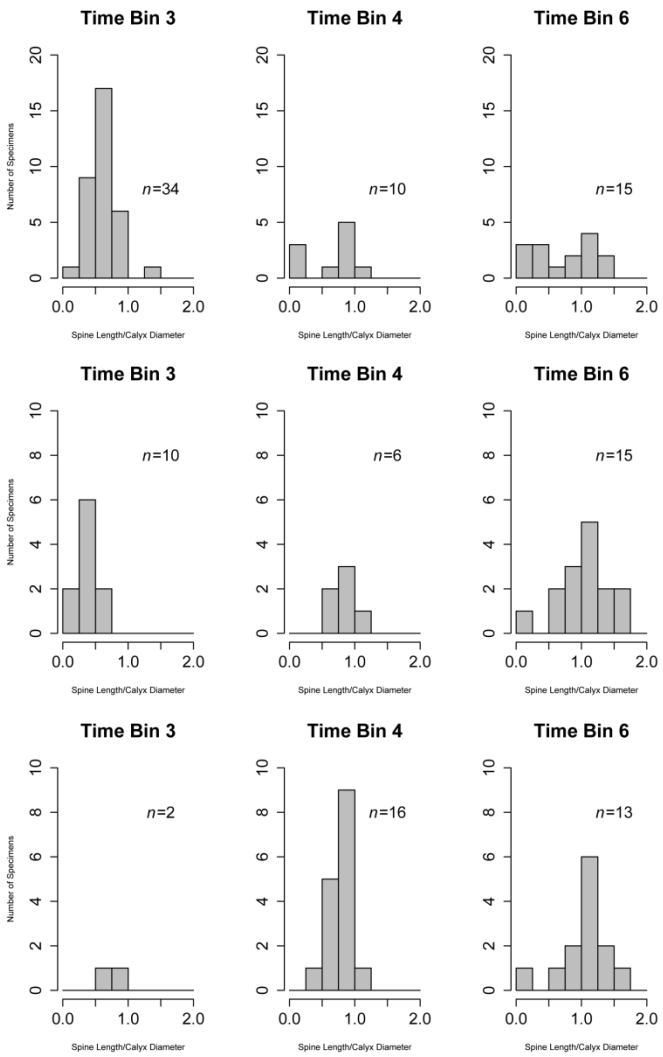

Figure 6. Spine length/calyx diameter distributions of specimens of *Dorycrinus* in time bins 3 through 6.

The Kolmogorov-Smirnov tests indicated that the distribution functions of time bins 3 and 4 and 4 and 6 were drawn from the same distribution. In contrast, the change in spine length/calyx diameter values of the C ray spine from time bins 3 to 4 and 4 to 6 both have statistically significant increases. This may be evidence of predator driven directional change as the distribution changes from lower ratio values in time bin 3 to higher ratio values in time bin 4 and further increase to time bin 6.

The data for spine length/calyx diameter in the spine above the E-ray in *Dorycrinus* indicates that the values between time bin 3 and time bin 4 do not show evidence for directional change, using the Mann-Whitney *U* test and the Kolmogorov-Smirnov tests. From time bin 4 to

time bin 6 there is no statistically significant change in the distribution functions, however, there is a statistically significant increase in trait values. This mirrors the trend observed in the spine above the C ray, which has evidence that the tegmenal spines situated above the arm rays in *Dorycrinus* have evidence of directional evolution from the Tournasian to the Viséan. These increases in spine length may be due to the increased predation pressure of Mississippian durophagous fish and, thus, may be evidence of escalation or coevolution.

Future Work

It is important to distinguish between coevolution and escalation. Escalation is defined as adaptive change in one organism in response to another (Vermeij, 1987). In a predator prey arms-race, escalation often focuses on the role of the predator as a driver of the evolution of prey, and downplays the role of the prey taxon in the evolution of the predator (Dietl and Kelly, 2002, Dietl, 2003). Coevolution, however, is an evolutionary response in two (or more) organisms in response to each other (Dietl and Kelly, 2002, Dietl, 2003). Because the spines present above the C and E rays of *Dorycrinus* were presumably capable of injuring any hungry fish that decided to crush their calices (See Hlavin, 1990 for an example of the deadly impact spines can have on a predator), it is logical to consider these taxa as dangerous prey (Brodie and Brodie, 1999, Dietl and Kelly, 2002) and thus according to Brodie and Brodie (1999) coevolution rather than just escalation might be expected between these crinoids and their durophagous fish predators. Further examiniation of the teeth and bite strength of these durophagous fishes is necessary. However, in order to make the claim that coevolution was occurring and given the data presented here, it is only valid to make a strong claim for escalation. Further study of microevolutionary trends in post-Givetian extinction and pre-Hangenberg interval are necessary to further determine the extent of escalation in crinoids before the

Tournasian rise in diversity. These will be conducted in addition to further study of the herein studied taxa in a phylogenetic context. In order to further study observed trends, within *Aorocrinus*, *Agaricocrinus*, and *Dorycrinus*, it will be first necessary to gain an understanding of the phylogenetic relationships of species within each genus and then to examine observed trends phylogenetically ascertained lineages.

Conclusion

Although not all of the observed genera behaved the same way in response to predation from durophagous fish, because there is evidence of escalation within the genus *Dorycrinus*, there is evidence of escalation in crinoids due to predatory pressures within the Lower Mississippian. Because the trend of increasing spine length was observed in the radial spines of *Dorycrinus*, this newly documented microevolutionary trend matches the generic level, macroevolutionary trend documented by Sallan et al. (2011). Because of this paired microevolutionary and macroevolutionary increase, this study provides evidence for a linkage of these two evolutionary processes, and may document the importance of ecological interaction on macroevolutionary trends.

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Appendix

Species	Spine Length/Calyx Diameter	*n*	Time Bin	Average Age of Time Bin (in MYA)
Aorocrinus banffensis	0.009090909	1	3	350.6
Aorocrinus elegans	0.075779037	1	3	350.6
Aorocrinus immaturus	0.194016908	2	1	364.3
Aorocrinus kelloggi	0.08742651	5	6	344.6
Aorocrinus parvibasis	0.13608871	1	1	364.3
Aorocrinus sp.	0.031243155	14	4	346.05
Aorocrinus radiatus	0.161971831	1	1	364.3
Aorocrinus subaculeatus	0.363246756	5	3	350.6
Aorocrinus suboviformis	0.01167402	5	3 or 4	350.6 or 346.05
Aorocrinus wachsmuthi	0.101712396	8	3	350.6

Table 2. Mean spine length/calyx diameter for all examined species of Aorocrinus.

Species	Mean Central Spine Length/Calyx Diame	*n*	Mean Ray C Spine Length/Calyx Diameter	*n*	Mean Ray E Spine Length/Calyx Diameter	*n*	Time Bin
Dorycrinus cornigerus	0.8521528	3	0.8659449	2	0.7605696	7	4
Dorycrinus gouldi	1.060925	3	0.9772864	2	1.017161	2	6
Dorycrinus intermedius	0.8998944	1	0.8259188	1	-	-	4
Dorycrinus mississippien	0.6384697	12	1.064765	13	1.056898	11	6
Dorycrinus missouriensis	0.2091997	3	0.8163294	3	0.8560425	5	4
Dorycrinus quinquelobus	0.9574724	3	-		0.8031661	4	4
Dorycrinus subturbinatu	0.9325284	1	0.5263819	1	0.7464931	2	3
Dorycrinus unicornis	0.5943327	33	0.3432418	9	-	-	3

Table 3. Mean Spine length/calyx diameter for all examined species of *Dorycrinus.*

Time Bin	Mean Convexity of PS1 in *Agaricocrinus* in pixels^{-1}	*n*	Mean Convexity of PS3 in *Agaricocrinus* in pixels^{-1}	*n*
1	0.00523074	5	0.003743871	7
3	0.01119329	42	0.00780913	38
3 or 4	0.011335	4	0.00673555	4
4	0.008577389	45	0.008141855	44
6	0.005385769	91	0.006733025	76

Mean Spine Length/Calyx Diameter in *Aorocrinus*	*n*	Mean Cental Spine Length/Calyx Diameter in *Dorycrinus*	*n*
0.1715236	4	-	-
0.1809869	15	0.6042796	34
0.01167402	5	-	-
0.03124316	14	0.6956369	10
0.08742651	5	0.7229607	15

Mean Ray C Spine/Calyx Diameter in *Dorycrinus*	*n*	Mean Ray E Spine/Calyx Diameter in *Dorycrinus*	*n*
-	-	-	-
0.3615558	10	0.7464931	2
-	-	-	-
0.8344661	6	0.801054	16
1.053102	15	1.050785	13

Table 4. Mean trait values for each time bin for all traits examined.

Taxon	Trait	Distributions Compared	*Mann-Whitney U*	*p*-value
Agaricocrinus	PS1	Time bin 3 (*n* =42) to Time bin 1 (*n* =5)	170	0.0113
Agaricocrinus	PS1	Time bin 4 (*n* =45) to Time bin 3 (*n* =42)	640	0.9955
Agaricocrinus	PS1	Time bin 6 (*n* =91) to Time bin 4 (*n* =45)	1175	1
Agaricocrinus	PS3	Time bin 3 (*n* =38) to Time bin 1 (*n* =7)	210	0.007066
Agaricocrinus	PS3	Time bin 4 (*n* =44) to Time bin 3 (*n* =38)	882	0.3369
Agaricocrinus	PS3	Time bin 6 (*n* =76) to Time bin 4 (*n* =44)	1322	0.9719
Aorocrinus	Spine Length/Calyx Diameter	Time bin 3 (*n* =15) to Time bin 1 (*n* =4)	20	0.8465
Aorocrinus	Spine Length/Calyx Diameter	Time bin 4 (*n* =14) to Time bin 3 (*n* =15)	16	1
Aorocrinus	Spine Length/Calyx Diameter	Time bin 6 (*n* =5) to Time bin 4 (*n* =14)	50	0.09297
Dorycrinus	Center Spine Length/Calyx Diameter	Time bin 4 (*n* =10) to Time bin 3 (*n* =34)	213	0.119
Dorycrinus	Center Spine Length/Calyx Diameter	Time bin 6 (*n* =15) to Time bin 4 (*n* =10)	89	0.2306
Dorycrinus	C Ray Spine Length/Calyx Diameter	Time bin 4 (*n* =6) to Time bin 3 (*n* =10)	60	0.0001249
Dorycrinus	C Ray Spine Length/Calyx Diameter	Time bin 6 (*n* =15) to Time bin 4 (*n* =6)	67	0.04742
Dorycrinus	E Ray Spine Length/Calyx Diameter	Time bin 4 (*n* =16) to Time bin 3 (*n* =2)	19	0.366
Dorycrinus	E Ray Spine Length/Calyx Diameter	Time bin 6 (*n* =13) to Time bin 4 (*n* =16)	169	0.001755

Table 5. Mann-Whitney *U* test results.

Taxon	Trait	Distributions Compared	*D*-Statistic	*p*-Value	Bootstrap *p*-Value
Agaricocrinus	PS1	Time bin 3 (*n* =42) to Time bin 1 (*n* =5)	0	1	1
Agaricocrinus	PS1	Time bin 4 (*n* =45) to Time bin 3 (*n* =42)	0.3619	0.003377	0.002
Agaricocrinus	PS1	Time bin 6 (*n* =91) to Time bin 4 (*n* =45)	0.4151	.00003109	0
Agaricocrinus	PS3	Time bin 3 (*n* =38) to Time bin 1 (*n* =7)	0	1	1
Agaricocrinus	PS3	Time bin 4 (*n* =44) to Time bin 3 (*n* =38)	0.0694	0.8218	0.734
Agaricocrinus	PS3	Time bin 6 (*n* =76) to Time bin 4 (*n* =44)	0.1986	0.1111	0.083
Aorocrinus	Spine Length/Calyx Diameter	Time bin 3 (*n* =15) to Time bin 1 (*n* =4)	0.6667	0.06038	0.029
Aorocrinus	Spine Length/Calyx Diameter	Time bin 4 (*n* =14) to Time bin 3 (*n* =15)	0.8619	.00002125	0
Aorocrinus	Spine Length/Calyx Diameter	Time bin 6 (*n* =5) to Time bin 4 (*n* =14)	0	1	1
Dorycrinus	Center Spine Length/Calyx Diameter	Time bin 4 (*n* =10) to Time bin 3 (*n* =34)	0.3	0.2488	0.182
Dorycrinus	Center Spine Length/Calyx Diameter	Time bin 6 (*n* =15) to Time bin 4 (*n* =10)	0.1667	0.7165	0.607
Dorycrinus	C Ray Spine Length/Calyx Diameter	Time bin 4 (*n* =6) to Time bin 3 (*n* =10)	0	1	1
Dorycrinus	C Ray Spine Length/Calyx Diameter	Time bin 6 (*n* =15) to Time bin 4 (*n* =6)	0.0667	0.9626	0.884
Dorycrinus	E Ray Spine Length/Calyx Diameter	Time bin 4 (*n* =16) to Time bin 3 (*n* =2)	0.25	0.8007	0.7
Dorycrinus	E Ray Spine Length/Calyx Diameter	Time bin 6 (*n* =13) to Time bin 4 (*n* =16)	0.0769	0.9186	0.83

Table 6. Kolmogorov-Smirnov test results.